

Diversification of a Food-Mimicking Male Ornament via Sensory Drive

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Summary

The evolutionary divergence of sexual signals is often important during the formation of new animal species, but our understanding of the origin of signal diversity is limited [1, 2]. Sensory drive, the optimization of communication signal efficiency through matching to the local environment, has been highlighted as a potential promoter of diversification and speciation [3]. The swordtail characin (*Corynopoma riisei*) is a tropical fish in which males display a flag-like ornament that elicits female foraging behavior during courtship. We show that the shape of the male ornament covaries with female diet across natural populations. More specifically, natural populations in which the female diet is more dominated by ants exhibit male ornaments more similar to the shape of an ant. Feeding experiments confirm that females habituated to a diet of ants prefer to bite at male ornaments from populations with a diet more dominated by ants. Our results show that the male ornament functions as a “fishing lure” that is diversifying in shape to match local variation in female search images employed during foraging. This direct link between variation in female feeding ecology and the evolutionary diversification of male sexual ornaments suggests that sensory drive may be a common engine of signal divergence.

Results

Sensory drive, broadly defined as the evolution of communication systems through adaptation to local environmental conditions, has been suggested to be an important promoter of signal diversification through selection to maximize signal efficiency [3–6]. Given enough variation among populations in the ecological variables that directly or indirectly affect signal efficacy, sensory drive could generate divergence in signal traits (e.g., sexual ornaments) and cause speciation when signals are involved in mate choice [6–11]. So far, demonstrations of divergence through sensory drive have been restricted to variation in signals that covary with the physical and structural properties of the habitat: the relationship between male coloration and local light conditions in sticklebacks and cichlid fishes [8, 10], the relationship between body coloration and the structural properties of the signaling background across chameleon species [12], and the interspecific correlation between male song and acoustic conditions in Amazonian song birds [11]. Yet, there are good reasons to believe that biotic factors may indirectly play a key role in sensory drive

[13, 14]. This would be the case whenever signal efficacy is affected by perception adaptations in the receiver that directly reflect environmental variation in factors such as local food abundance or predator fauna [15]. It has, for example, been suggested that evolutionary diversification of color ornamentation in nectarivorous and frugivorous birds originated by color matching to various flowers and fruits utilized as food resources (e.g., [16, 17]). Here, we investigated whether variation in feeding ecology generates sensory drive on male sexual ornament morphology in the swordtail characin (*Corynopoma riisei*). This small freshwater fish is common in streams in Trinidad and northern Venezuela [18]. Males are equipped with a flag-like ornament on each operculum that they display during courtship (Figure 1). Females react to the flag ornament as they would to a food item, biting vigorously at the ornament and thereby positioning themselves in a manner allowing sperm transfer to females [19]. Fertilization is internal, and females store viable sperm for many months [19]. The remarkable sexual dimorphism in this species has been suggested to result from sensory exploitation, whereby the male opercular flag ornament functions as a food mimic [20–23].

Recent work on this species has revealed that Trinidadian populations are genetically distinct and that the shape of the male ornament varies strikingly across populations [23]. The swordtail characin feeds mainly on uniformly sized terrestrial invertebrates that fall onto the water surface from the surrounding vegetation, and the diet is heavily dominated by arboreal ants, which make up about 50% of all prey items [24]. Other common prey items are beetles (adults and larvae), springtails, and dipteran larvae. Importantly, female food utilization varies across populations chiefly in the proportion of prey items that are ants, ranging from about 10% to 75% [24]. The terrestrial input of ants varies consistently across streams in Trinidad (see Discussion), and swordtail characin populations inhabiting wider streams with more canopy cover have a larger proportion of ants in the diet [24]. Here, we posited that the observed differentiation of the male sexual signal [23] is generated by sensory drive, where variation in the shape of the flag ornament has evolved to match environmentally imposed local variation in the search images that females employ during foraging. To test this hypothesis, we performed (1) a comparative study of covariation between male ornament shape and female food utilization across 17 natural populations in Trinidad and (2) a set of experiments where we assessed whether female food habituation affects their attraction to male ornaments.

Covariation between Female Diet and Male Ornamentation across Wild Populations

We characterized the shape of male ornaments from different populations using elliptical Fourier analysis [25] and then tested for an association between the shape of the flag ornament and female diet across populations, using canonical correlation analysis (see Supplemental Experimental Procedures for full descriptions of shape and gut content analyses). We found that female food utilization indeed covaried with the shape of the male ornament across populations (whole set correlation $R^2_{X,Y} = 0.986$, Rao's $F_{25,27.5} = 2.367$, $p = 0.015$). A closer

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Figure 1. Courtship in the Swordtail Characin
Male (right) displaying his opercular flag ornament in front of a female (left), who moves in to bite at the ornament.

inspection of this covariation revealed a tight correlation between the first pair of canonical variables (see Figure 2) and showed that ornaments in populations where females forage more on ants were more tapered and curved toward the distal end compared to populations where females forage primarily on other prey items. These precise shape characteristics also define the outline of a typical ant, where the thick abdomen tapers off toward the anterior end and the ventral margin is concave whereas the dorsal is convex [26] (Figure 2). This contrasts with the shape of beetles, the second most common prey item [24], which is oval and more uniform.

However, a covariation across populations between ornament morphology and female diet is necessary but not sufficient evidence for our hypothesis. A direct comparative test of sensory drive through food mimicry must also demonstrate that such a covariation describes a resemblance between the male ornament and the mimicked food item, using objective measures of resemblance. In order to provide a comparative test of whether the male flag ornament of the swordtail characin mimics an ant, we assessed the relationship between (1) shape similarity between the population-specific average ornament and the average shape of an ant (extracted from female guts) on one hand and (2) proportion of ants in the female diet on the other. We found that the overall shape similarity between the flag ornament and an ant was significantly correlated with the proportion of prey items that were ants across populations (Figure 3). Thus, ornaments were indeed most ant-like in populations where females forage most on ants.

Female Foraging Experience and Preference for Male Ornaments

We performed two laboratory experiments testing the shared prediction that male flag ornaments from populations where female diet is dominated by ants are more efficient at attracting the attention of females that have been habituated to forage on ants. For this, we used captive-reared animals

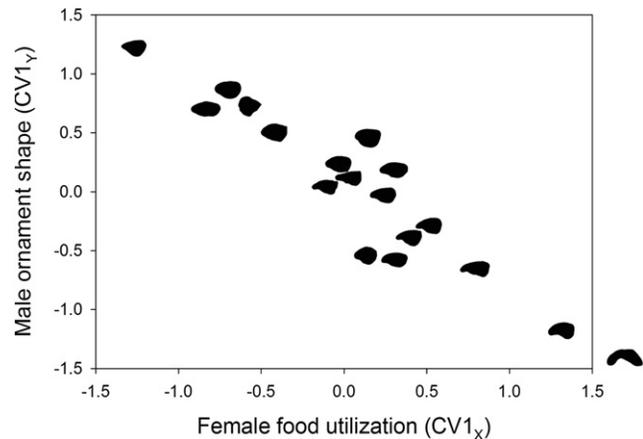


Figure 2. Female Diet Covaries with Male Ornament Morphology across Populations

Populations are ordinated along the first pair of canonical variables ($R_c = 0.918$, $\chi^2_{25} = 44.77$, $p = 0.009$), and symbols depict the mean outline of the male ornament in each population. Here, female food utilization ($CV1_x$) is positively correlated across populations with the average proportion of female prey items that are ants ($r = 0.66$, $p = 0.004$), such that females in population located further to the right in this ordination space forage more on ants, whereas those in populations further to the left forage more on other invertebrate prey items (e.g., beetles [$r = -0.42$]). The second pair of canonical variables (data not shown) was not statistically significant ($\chi^2_{16} = 25.31$, $p = 0.065$). Inserted at the lower right, outside of the ordination space, is the mean outline of an ant (from a sample of ants from female guts) for comparison. See Supplemental Experimental Procedures for full description of analyses.

from an aquarium stock that were naive to foraging on ants prior to the experiment, to standardize previous female feeding history, thus ensuring that any effect would be due to food habitation during the experiment. We allowed one group of adult females to feed on ants by presenting ants onto the water surface while a second group of females were fed other food items. We then recorded the behavior of these females in choice tests where they were presented with two ablated male ornaments simultaneously: one from a male of a population where the diet consisted mostly of ants, and another from a male of a population with few ants in the diet (see Supplemental Experimental Procedures for full description of experimental design). As predicted, females habituated to eating ants directed a larger proportion of bites toward male flag ornaments derived from populations in which the female diet was dominated by ants (Figure 4). These experiments thus confirmed the hypothesis that male flag ornaments from populations where females eat more ants not only are more similar to ants but are actually more efficient at attracting the attention of females that are habituated to eating ants.

Discussion

Whenever male signals have evolved to mimic female food items through sensory exploitation, divergence of male signals through sensory drive is predicted when female food utilization varies across populations. We first note that our results provide evidence for sensory exploitation. They suggest that the shape of the male flag ornament of the swordtail characin has evolved to track the search images that females employ in foraging and that the ornament thus essentially functions as a “fishing lure” aimed at attracting the attention of females.

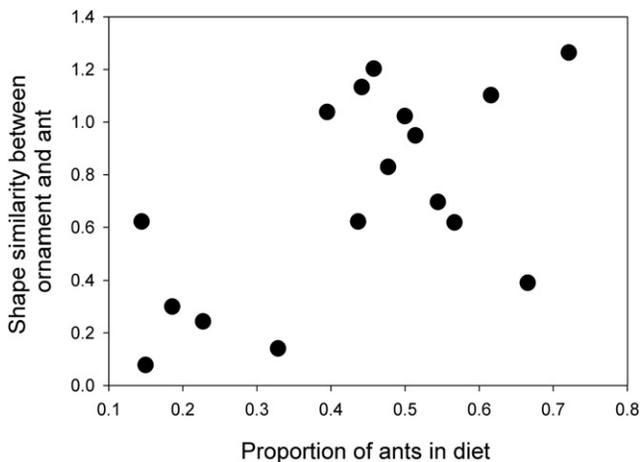


Figure 3. Male Ornaments Are More Ant-like in Populations Where Females Forage More on Ants

Relationship across populations between the proportion of ants in the diet of adult females and the similarity in average shape between the male ornament and an ant ($r_{17} = 0.60$, $p = 0.011$).

Several related fish species within the family Glandulocaudinae exhibit analogous, but not homologous, male ornaments [21]. Physical proximity and appropriate positioning of the female is important for successful sperm transfer in these internally fertilizing fish that lack external genitalia in males [19], and these male ornaments have likely evolved as a means for males to achieve the necessary proximity to their mates. The form of sensory exploitation [14] involved in the evolution of male ornaments in the swordtail characin bears similarities to male signals in, for example, water mites (where males vibrate their legs near females to mimic the movements of the copepod prey that females feed on [27]), Goodeinae fishes (where males in some species bear a larvae-like terminal yellow band on the tail that evokes feeding responses in females [28, 29]), guppies (where orange coloration in males may resemble orange-colored fruits that females occasionally feed upon [30]), and orchid bees (where males collect and emit fragrances of those flowers that females use as nectar sources [31]). Sensory exploitation is, however, not synonymous with sensory drive [6, 14]. Future studies of systems such as those above, where signals have evolved at least in part by sensory exploitation, could test whether sensory drive is a common outcome of biotic variation.

The results of our experimental food habituation show that the modulation of female food preference for male flag ornaments reflects, at least initially, a phenotypically plastic response to local food abundance. After even a brief period of food habituation (10 days), previously naive females responded to the food habituation treatment. This is in line with a general role for phenotypic plasticity in diversification [32]. Here, plastic responses in the signal receiver would generate variation in the sexual selection regimes experienced by the signalers. For this mechanism to result in signal diversification, two conditions must be met. First, some level of temporal stability in food composition is required for signal diversification to evolve. This condition is met in the swordtail characin: ants represent a large proportion of the terrestrial invertebrate input into Trinidadian streams, and there are marked and significant differences across streams in this proportion [33]. Moreover, this variation is consistent over

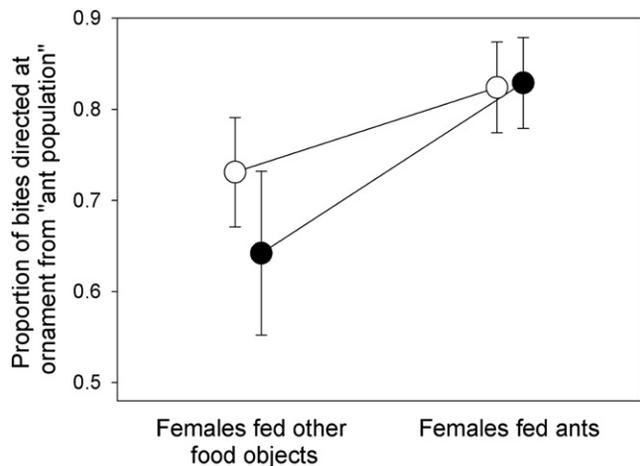


Figure 4. Females Habituated to Feeding on Ants Bite More Often at Flag Ornaments of Males from Populations with a Female Diet Rich in Ants

Proportion of bites directed at ornaments from populations with a diet rich in ants in two independent experiments (●, experiment 1; ○, experiment 2), when females were given a choice between an ornament from a population with a diet rich in ants and an ornament from a population with a diet containing few ants. Females habituated to a diet of ants prior to these trials showed a preference for biting at ornaments from populations with a higher proportion of ants in the female diet, compared to females habituated to other food items (experiment 1 [ants versus flake food]: $\chi^2_1 = 3.49$; experiment 2 [ants versus *Drosophila* larvae]: $\chi^2_1 = 1.57$) (two-tailed weighted Z combined probability; $p = 0.031$). Error bars represent estimates of standard error. See Supplemental Experimental Procedures for full description of experimental design and statistical analyses.

time when seasonal variation in terrestrial input is taken into account [33]. In fact, physical environmental features of streams predict terrestrial invertebrate input and, consequently, the composition of female diet across populations [24, 33]. Second, gene flow between populations must be limited, to allow for genetic differentiation. Again, this condition is met in the studied populations of the swordtail characin: analyses based on neutral genetic markers have revealed extensive genetic structuring even within single river drainages [23].

The results of our study of the swordtail characin are consistent with the predicted effect of variation in feeding ecology on diversification of a sexual signal through sensory drive. This suggests that interpopulation environmental variation in biotic factors can, in principle, generate diversification through sensory drive even in the absence of differences in abiotic factors. Furthermore, our results also blur the distinction between female food preferences and female mate preferences [27] and provide an example of how the concerted effects of natural and sexual selection can generate signal divergence [34]. In light of the fact that environmental variation is omnipresent, variation in variables such as food abundance or predator/parasite fauna may commonly trigger the divergent evolution of signal design through its effect on signal perception among receivers. We suggest that this form of sensory drive is an unappreciated source of signal diversification.

Supplemental Information

Supplemental Information includes one figure, one table, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2012.05.050>.

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